Defoliation of the Invasive Tree *Falcataria moluccana* on Hawaii Island by the Native Koa Looper Moth (Geometridae: *Scotorythra paludicola*), and Evaluation of Five Fabaceous Trees as Larval Hostplants

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Abstract. The koa looper (Geometridae: *Scotorythra paludicola*) is an endemic Hawaiian moth whose caterpillars feed on *Acacia koa*, and experience occasional outbreaks, producing vast defoliations of forests. During an extensive and ongoing outbreak of this species on the island of Hawaii, patchy defoliation of *Falcataria moluccana* ("albizia") was observed in the vicinity of Akaka Falls State Park, relatively distant from the main defoliation of koa, raising questions about the host range of the koa looper. To identify suitable host plants in the laboratory, we offered the koa looper foliage from five fabaceous tree species (*A. koa, A. confusa, F. moluccana, Prosopis pallida,* and *Leucaena leucocephala*), and recorded feeding and performance on these diets. Among the five tree species, only *A. koa* and *F. moluccana* were accepted as food; caterpillars on the other three species all died by the fifth day of the trial. Survival of the koa looper to pupation and adulthood on *F. moluccana* did not differ significantly from that on *A. koa* phyllodes, indicating that this tree is a suitable host, though it does not appear to be widely utilized in the field. Both oviposition preference and larval requirements are likely important determinants of the realized diet breadth for the koa looper. Additionally, development times at 19°C on *A. koa* and *F. moluccana* were nearly twice as long as at 23°C, highlighting the importance of temperature for development of this insect.

Key words: Lepidoptera, host suitability, feeding assay, host shift

Background

The endemic koa looper moth, *Scotorythra paludicola* (Butler) (Geometridae) is considered a specialist on foliage of the hardwood tree koa, *Acacia koa* Gray (Fabaceae) (Zimmerman 1958), one of the most important native trees in Hawaii ecologically, culturally, and economically (Elevitch et al. 2006). The koa looper is an eruptive insect, experiencing occasional, unpredictable population explosions on the islands of Maui and Hawaii, during which vast expanses of koa forest are defoliated (Zimmerman 1958, Haines et al. 2009). A massive outbreak of this species is currently underway on the island of Hawaii. Defoliation was first detected in January 2013 in the forests above the Hilo and Hamakua Districts, and moth populations have remained high for multiple generations, dispersing across the island to affect most major tracts of koa. As of

October 2013, the outbreak is ongoing; it has defoliated approximately 70,000 acres of forest, making this the largest koa looper outbreak ever documented.

Although caterpillars of the koa looper will feed on plants other than koa during outbreaks (Fullaway 1947, Haines et al. 2009), this has only been reported on non-host trees or shrubs adjacent to or beneath koa trees that have been defoliated, and is by late-instar caterpillars that have depleted the supply of koa phyllodes and then dropped out of the canopy to seek other sources of food. This is consistent with observations from the current outbreak; we observed fourth and fifth-instar caterpillars feeding on strawberry guava (Myrtaceae: *Psidium cattleianum* Sabine), Koster's curse (Melastomataceae: *Clidemia hirta* [L.]), and ohia lehua (Myrtaceae: *Metrosideros polymorpha* Gaudich.) at Humuula Trail, and mao hau hele (Malvaceae: *Hibiscus brackenridgei* Gray) at Puu Waawaa after the koa canopy had been defoliated.

In mid-March 2013, staff at Akaka Falls State Park (Honomu, HI, 350 m) reported heavy defoliation of *Falcataria moluccana* (Miquel) to the Hawaii Department of Agriculture (HDOA). This large fabaceous tree, commonly known as albizia, is native to Indonesia and New Guinea, and is considered invasive in Hawaii and other Pacific Islands (Global Invasive Species Database 2008). The observed defoliation was localized, despite *F. moluccana* being common and occurring in dense stands throughout the area. About 10–12 large (about 20 m tall) trees were noticeably affected: one patch near the falls inside the park itself (N19.8540, W155.1535), and a second patch outside of the park about 100 m south of the parking area (N19.8528, W155.1526). Late-instar caterpillars were extremely abundant during the last week of March, dropping out of trees and accumulating on handrails (Fig. 1). During

Figure 1. A young visitor watches caterpillars crawling on the handrails at Akaka Falls State Park on March 22, 2013. (Photo: Anastasia Poland).

a site visit on 28 March, Conant found that caterpillars were fewer, but still easily found in the understory beneath defoliated *F. moluccana* trees, and some were observed feeding on white ginger (*Hedychium cornarianum* Koenig). Many of the caterpillars appeared to be sickly, but it was unknown whether this was due to starvation or disease. A sample of caterpillars was collected by Conant, reared by P. Banko (USGS) and confirmed by Haines as the koa looper. By the end of March, most of the affected trees were completely defoliated (Fig. 2) and caterpillars were no longer present. Groundskeepers and parking attendants did not observe any unusual moth activity at the site (unlike

Figure 2. A defoliated *Falcataria moluccana* tree at Akaka Falls State Park on March 27, 2013. (Photo: Jon McClintock)

the mass emergences of moths seen in koa forests within weeks of defoliation), so it was uncertain whether *F. moluccana* was capable of supporting complete development of caterpillars to adulthood. After March, no additional generations of caterpillars were observed within the park. All defoliated trees reflushed leaves over the course of several months. By October 2013, some trees were producing flowers, although many branches remained bare, perhaps due to dieback of entire branches.

In an email to the University of Hawaii Cooperative Extension Service, Douglas Toomey, the owner of a parcel of land immediately north of Akaka Falls State Park, reported defoliation of a stand of *F. molucanna* in March, around the same time as the Akaka Falls defoliation. This landowner farms bamboo shoots in the understory of the affected trees, and was concerned that the caterpillars might also feed on bamboo. In a follow up interview with Toomey in November 2013, he indicated that the affected stand was about 4 ha in total, located about 750 m from the affected trees in Akaka Falls State Park. The defoliation appeared to begin in the center of the stand and spread outward, ultimately defoliating most of the trees. Individual trees were either severely defoliated or appeared completely unaffected, consistent with the patchiness observed at Akaka Falls. Trees on the periphery of the stand were not affected by caterpillars, and he saw no evidence of damage to other plant species. Toomey reported that defoliated trees remained bare for many months, first beginning to reflush around September 2013. Interestingly, he indicated that he has two 15-year-old koa trees on his property, located about 400 m away from the affected *F. moluccana* stand, and these appeared to be completely undamaged. A few months prior to the defoliation, Toomey observed an incredible abundance of moths attracted to lights at his home, completely covering his windows, unlike anything he had seen before. This is similar to reports from other regions around the island during the outbreak, and these were likely swarms of koa looper moths. He recalled that this occurred in January 2013, which seems somewhat early to be the source of caterpillars causing defoliation in late March, based on what we know about the life cycle of the caterpillars; eggs hatch

in about one week in the laboratory, and caterpillar development takes up to one month (Haines et al. 2009, and see below).

Additionally, a helicopter survey conducted on 6 Feb 2013 by the Hawaii Department of Land and Natural Resources identified patches of defoliated *F. moluccana* about 2 km southwest of Akaka Falls, in forests where it was the dominant canopy tree (600–650 m, N 19.84°, W 155.17°, K. Magnacca, pers. comm.). This tract of *F. moluccana* was adjacent to the main defoliation of koa forest, and encompassed an area of about 1 km², though the defoliation within that area was patchy, similar to what was observed at Akaka Falls. At the time of the aerial survey, the cause of the defoliation was uncertain, but given the later observations in the vicinity of Akaka Falls, it is highly likely that the koa looper was responsible. Defoliation of *F. moluccana* elsewhere on the island has not been noted, though it is possible that additional occurrences have gone undetected.

According to groundskeeping staff at Akaka Falls State Park, there is no koa planted or occurring naturally in the park, nor are there any large stands of koa within 2 km, so the defoliation of *F. moluccana* could not have been "spillover" damage from caterpillars moving off of defoliated koa. Therefore, we assume that female moths actively laid eggs on the trees. This is the first report of a plant other than koa being targeted by female moths and supporting development of koa looper caterpillars from hatching through at least late instars.

The defoliation of *F. moluccana* raised questions about the overall host specificity of the koa looper, and whether other common species of fabaceous trees may support populations of caterpillars, especially during outbreaks. Several invasive trees and shrubs in the family Fabaceae can form dense stands, and these occur in both dry and wet habitats, making it likely that they could be encountered by the koa looper. The host specificity of phytophagous insects can be determined by plant traits that affect larvae (e.g., feeding stimulants, deterrents, toxins, or nutrients), adult females (e.g. oviposition stimulants and deterrents, plant volatiles, or visual cues), or a combination of both of these (Stadler et al. 1995, Mayhew 2001, Scheirs and De Bruyn 2002), and host acceptance by ovipositing females does not always imply host suitability for larvae (Renwick et al. 2001, Gripenberg et al. 2010, Walter et al. 2010). Female *Scotorythra* moths, including the koa looper, lay eggs in the bark or moss on the trunks of host trees (Zimmerman 1958, WPH, pers. obs.), but specific oviposition cues are unknown. Host specificity of the caterpillars has not been previously studied. To explore the role of larval requirements in the host specificity of the koa looper, we performed laboratory assays to answer the following questions:

(1) Are other common fabaceous species recognized as food plants by koa looper caterpillars?

(2) How does survival and performance of koa looper caterpillars compare on *A. koa* and different fabaceous species?

(3) Is the koa looper capable of completing full development on *F. moluccana*?

Materials and Methods

Source of foliage. We compared caterpillar performance on koa (*A. koa*) foliage to that on four non-native fabaceous trees commonly occurring in Hawaii: *F. moluccana*, Formosan koa (*Acacia confusa* Merr.), koa haole or white leadtree (*Leucaena leucocephala* [Lam.]), and kiawe (*Prosopis pallida* Humb. & Bonpl. ex Willd.). We haphazardly collected branches with new growth from mature trees in Manoa, Honolulu, HI, collecting from several individual trees of each spe-

cies. Foliage was kept moist and refrigerated at 4°C until its use in trials, within one week of collection. For the two *Acacia* species, the primary photosynthetic tissue of mature trees (i.e., the functional "leaves") is flattened petioles called phyllodes, and these were used for trials. The other three plant species do not produce phyllodes, and therefore true leaves were used. Young, fully expanded leaves or phyllodes were used for each plant species.

Source of caterpillars. Koa looper caterpillars were obtained from eggs laid by wild-caught female moths. About 40 female moths were collected from swarms of dispersing moths in Ocean View Estates subdivision in the District of Kau, HI (N 19.142°, W 155.761°) on 20 Jul 2013. Female moths were housed in screen cages with moss clumps, sections of koa bark, and koa foliage (as a potential oviposition cue) for 5 days. They were fed sugar water sprayed on damp paper towels draped over the cages. Moss clumps and koa bark were removed daily after overnight exposure to moths, and placed in 35-oz plastic tubs without food until the eggs hatched (6–7 days at 22°C). Neonate caterpillars were removed from tubs and used in trials within 24 hours of hatching.

Feeding trials. We conducted a no-choice assay to assess host suitability. We randomly assigned naïve caterpillars to treatments (N = 15 per treatment for all plants except *F. moluccana*, for which N = 14 due to one caterpillar escaping partway through the trial). We placed them individually in 2-oz serving cups lined with 4.25-cm filter paper (moistened initially with 200 µL of water) and added one leaf or phyllode to each cup. Initially, we replaced foliage every two days, but as caterpillars grew larger and consumed food more rapidly towards the end of the trial, we replaced foliage daily. Filter paper was remoistened and replaced as needed to maintain high humidity and cleanliness in

the cups, and frass was removed every two days. Each day we recorded survival and any evidence of feeding (e.g., leaf damage and frass production). When caterpillars pupated, we weighed them and determined their sex by examining the genitalia visible on the terminal abdominal segments. This assay was conducted at an ambient laboratory temperature of 23°C.

We also report data from a second trial conducted simultaneously, but in a different laboratory. While the trial described above compared five different trees, the second dataset was obtained as part of a larger study designed to compare the performance of caterpillars on different types of koa foliage (Barton and Haines 2013). This second trial compared performance of caterpillars (from the same batch as above) on mature *F. moluccana* leaves (N = 10) and on various types of koa foliage: young phyllodes (N = 47), mature phyllodes (N = 48), and true leaves (N = 43). For this trial, subjects were frozen upon pupation, so duration of the pupal stage and adult emergence were not measured, and the response variables were percent survival to pupation, duration of larval development, and pupal weight. The second trial was conducted at 19°C, and therefore data from the two trials were not directly comparable.

Data analysis. All analyses were performed in Minitab 14 (Minitab Inc., State College, PA). Due to small sample sizes, we did not feel it was appropriate to conduct formal survivorship analyses at each point in the time series, to explore fine-scale differences in performance among the diets. We instead were interested in overall indicators of performance on each diet. For plants that were accepted as food plants (*A. koa* and *F. moluccana*), we compared proportions of caterpillars surviving to pupation and to adulthood using Fisher's exact tests with a threshold of significance of 0.05. We compared

duration of larval development, duration of pupal stage, and pupal weight using ANOVAs with diet and sex as the independent variables.

For the second trial, which compared *F. moluccana* to three different foliage types of *A. koa*, we performed a Bonferroni-adjustment on our threshold of significance for Fisher's exact tests on survival, to correct for multiple comparisons. For pairwise comparisons of pupal weight and duration of larval development, we used Dunnett's post-hoc test to compare performance on each of the three foliage types to performance on *F. moluccana*.

Results

Feeding. Of the five plants tested, only *A. koa* and *F. moluccana* were suitable host plants for *S. paludicola* caterpillars; 100% of caterpillars on both diets accepted them as food, and at least 50% survived to adulthood on each (Table 1). The other three plants were not suitable hosts, and all caterpillars in on these diets died by the fifth day of the assay (Fig. 3). Two of the plants, *A. confusa* and *P. pallida*, were completely unacceptable to neonate caterpillars, and we observed no evidence of feeding on them. Four of the fifteen caterpillars offered *L. leucocephala* initially recognized it as a food source, feeding and producing some frass during the first day of the trial, but feeding did not continue, and all these caterpillars died by the fifth day.

Survival. *A. koa* and *F. moluccana* supported complete development from hatching to adulthood in both trials. In the first trial (Fig. 3, Table 1), Fisher's exact tests found no significance differences between survival to pupation on *A. koa* (66.7%) and *F. moluccana* (78.6%) (P = 0.682), or survival to adulthood (*A. koa* = 66.7%, *F. moluccana* = 50%, P = 0.462). Similarly, in the second trial (Table 2), survival to pupation on *F. moluccana*

(80%) did not differ from that on *A. koa* young phyllodes (72.3%, P = 1.0) or mature phyllodes (72.7%, P = 1.0), but was significantly higher than survival on true leaves (32.6%, P = 0.011) (corrected α = 0.017 for three comparisons).

Development time. In the first trial (Table 1), larval development time did not differ on *A. koa* phyllodes (least squares mean = 15.6 ± 0.62 d) and *F. moluccana* leaves (least squares mean = 16.4 ± 0.57 d) ($F_{1, 18}$ = 0.87, P = 0.363). In the second trial (Table 2), larval development time on *F. moluccana* leaves (least squares mean = 34.3 ± 1.20 d) was significantly longer than on *A. koa* young phyllodes (least squares mean = 23.7 ± 0.58 d, P < 0.0001) and mature phyllodes (least squares mean = 27.8 ± 0.60 d, P < 0.0001), but not significantly different from development time on true leaves (least squares mean = 31.4 ± 0.93 d, P < 0.137). Duration of the pupal stage in the first trial (Table 1) was about one day longer on *F. moluccana* leaves (least squares mean = 11.2 ± 0.37 d) than on *A. koa* phyllodes (least squares mean = 10.2 ± 0.33 d), and this difference was significant ($F_{1, 14}$ = 4.87, P = 0.045).

There were significant differences in development time between sexes. In the first trial, mean larval development time was about 2 days longer for females (least squares mean = 16.9 ± 0.68 d) than for males (least squares mean = 15.0 ± 0.53 d) ($F_{1, 18}$ = 4.69, P = 0.044), while in the second trial, females (least squares mean = 31.3 ± 0.53 d) took about four days longer to develop than males (least squares mean = 27.3 ± 0.61 d) ($F_{1, 83}$ = 28.74, P < 0.0001). Notably, larval development at 19°C during the second trial took nearly twice as long as at 23°C in the first trial. The duration of the pupal stage in the first trial did not differ between males (least squares mean = 11.1 ± 0.30 d) and females (least squares mean = 10.3 ± 0.40 d) ($F_{1, 14}$ = 2.06, P = 0.173).

Table 1. Performance of koa looper caterpillars on five different fabaceous tree species, from a trial conducted at 23°C. For development times and pupal mass, least squares means are presented, which take into account differences due to sex. We tested for significant differences only between *Acacia koa* and *Falcataria moluccana*, since these were the only species caterpillars accepted as food.
* = significant difference from *F. moluccana* ($P < 0.05$).

Species	Foliage type	Sample size	Caterpillars that fed	Survived to pupation	Survived to adulthood	Mean development time (d) Larval	Pupal	Mean pupal mass (mg)
Acacia koa	Phyllodes	15	100%	66.7%	66.7%	15.6 ± 0.62	10.2 ± 0.33*	64.67 ± 3.87
Acacia confusa	Phyllodes	15	0	0	0	N/A	N/A	N/A
Falcataria moluccana	True leaves	14	100%	78.6%	50.0%	16.4 ± 0.57	11.2 ± 0.37	61.93 ± 3.55
Leucaena leucocephala	True leaves	15	26.7%	0	0	N/A	N/A	N/A
Prosopis pallida	True leaves	15	0	0	0	N/A	N/A	N/A

Table 2. Performance of koa looper caterpillars on *Falcataria moluccana* and different foliage types of *Acacia koa*, from a trial conducted at 19°C. For larval development time and pupal mass, least squares means are presented, which take into account differences due to sex. We tested for significant differences between each foliage type and *F. moluccana*.
* = significant difference from *F. moluccana* ($P < 0.05$).

Species	Foliage type	Sample size	Survived to pupation	Mean larval development time (days)	Mean pupal mass (mg)
Falcataria moluccana	True leaves	10	80.0%	34.3 ± 1.20	75.76 ± 5.83
Acacia koa	Young phyllodes	47	72.3%	23.7 ± 0.58*	73.58 ± 2.83
Acacia koa	Mature phyllodes	48	72.7%	27.8 ± 0.60*	84.32 ± 2.93
Acacia koa	True leaves	43	32.6%*	31.4 ± 0.93	77.48 ± 4.53

Pupal mass. There were no differences in pupal mass attained on *F. moluccana* and *A. koa* in either of the trials. In the first trial (Table 1), mean pupal mass on *F. moluccana* (least squares mean = 61.93 ± 3.55 mg) did not differ from that on *A. koa* (least squares mean = 64.67 ± 3.87 mg) ($F_{1, 18} = 0.28$, P = 0.604). In the second trial (Table 2), pupal mass on *F. moluccana* (least squares mean = 75.76 ± 5.83 mg) did not differ from that on *A. koa* young phyllodes (least squares mean = 73.58 ± 2.83 mg, P = 0.958), mature phyllodes (least squares mean = 84.32 ± 2.93 mg, P = 0.352), or true leaves (least squares mean = 77.48 ± 4.53 mg, P = 0.985). In both trials female pupae were much heavier than male pupae (*first trial*: least squares means females = 77.23 ± 4.21 mg, males = 49.37 ± 3.27 mg, $F_{1, 18} = 27.14$, P < 0.0001; *second trial*: least squares means females = 95.90 ± 2.57 mg, males = 59.67 ± 2.98 mg, $F_{1, 83} = 100.19$, P < 0.0001).

Discussion

Our results demonstrate that *F. moluccana* is not only an acceptable food source for koa looper caterpillars, but supports complete development from hatching to adulthood with a success rate similar to that on different types of *A. koa* foliage. Although our data suggested that development times are somewhat slower on *F. moluccana*, and perhaps that performance drops off during prepupation and pupation (Fig. 3), such fine-scale differences in performance would best be explored in more depth using larger sample sizes.

It is important to note that although *F. moluccana* is an adequate host plant, and was attacked by the koa looper during the current outbreak, damage to *F. moluccana* in the field appears to have been rare and patchy, despite this being a very common tree, growing densely in areas nearby defoliated koa. Factors that affect female oviposition are completely unknown,

and could play an important role in determining the realized host range for the koa looper. Defoliation of *A. koa* during outbreaks can also be somewhat patchy (Haines, personal observation), sometimes with small patches of trees defoliated, while nearby trees appear unaffected. This suggests either that female moths key in on certain trees due to desirable plant traits, or that they actively aggregate towards each other, resulting in patches of defoliation irrespective of host quality. Although female moths lay eggs in the bark and moss on the trunks of trees, it is not known how they recognize koa trees, nor is it known whether they can detect intraspecific variation in foliage quality. Ecological factors may also play a role in preventing *F. moluccana* from being more heavily utilized. For example, *F. moluccana* is densest at lower elevations, which may not be optimal habitat for the koa looper, either due to direct microclimate requirements or due to ecological interactions with other organisms such as parasitoids or ants.

Because *F. moluccana* is considered invasive, and is widespread at low elevations on the islands of Hawaii and Oahu, it is tempting to suggest that the koa looper may serve as a natural, native biological control agent for this tree. However, at this point we consider it unlikely that *S. paludicola* will significantly impact populations of *F. moluccana*, considering that defoliation of trees was rare and patchy, and koa looper outbreaks are historically rare events. Damage to *F. moluccana* appeared to be restricted to one region, despite millions of moths surely being present following defoliation of koa near dense *F. moluccana* forests elsewhere (e.g. the Saddle Road near Kaumana). However, we cannot rule out the possibility that this represents a recent host range expansion, and that defoliation of *F. moluccana* will become more frequent. Future defoliation
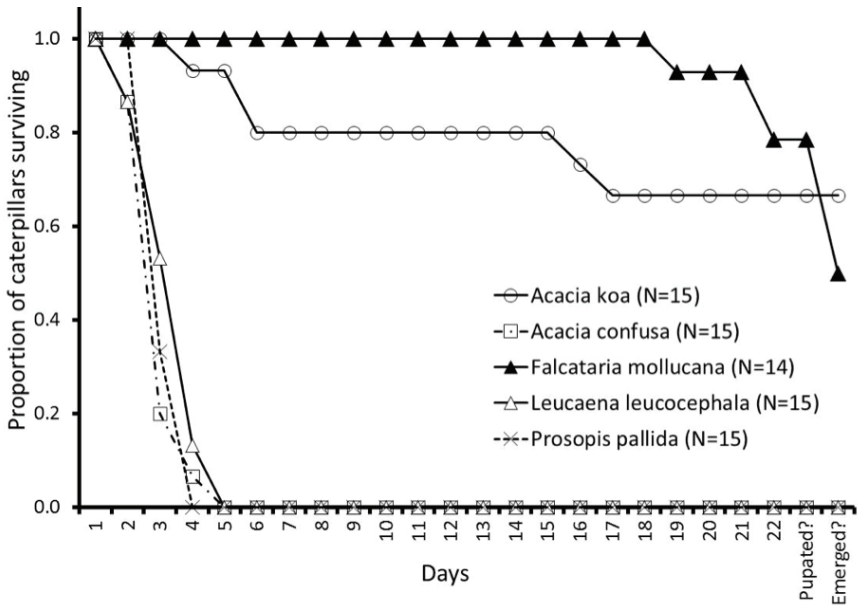
Figure 3. Survival of *Scotorythra paludicola* caterpillars on five diets at 23°C. Only *Acacia koa* and *Falcataria mollucana* were accepted as food, and both supported development to adulthood.

of this invasive tree should be documented, if it occurs.

Although *F. moluccana* appears to be a suitable host for *S. paludicola*, all of the other common fabaceous trees we tested were clearly unsuitable, indicating that host range in the koa looper is not simply constrained by oviposition preferences of female moths, but also limited by larval requirements. We cannot discern from our assays whether caterpillars virtually completely rejected *L. lecucocephala*, *P. pallida*, and *A. confusa* because they lacked the proper feeding stimulants or, alternatively, whether these plants possess chemical deterrents or toxins. It is particularly interesting that caterpillars refused *A. confusa*, which of the species tested, is the most phylogenetically and morphologically similar to *A. koa*; both species belong to the same subgenus (Brown et al. 2012), and are the only two

species in our study that bear phyllodes. Examination of the secondary chemistry of *A. koa* and its relatives may reveal important underlying traits that influence the feeding preferences of the koa looper, both among species and within *A. koa*. It would also be worthwhile to test other naturalized fabaceous trees such as monkeypod (*Albizia saman* F. Muell.) and black wattle (*Acacia mearnsii* De Wild.) to determine the full diet breadth of koa looper caterpillars, and identify which species could potentially be affected by defoliation in the field. Though much less common in Hawaii, Australian blackwood (*Acacia melanoxylon* R. Brown) would also be interesting to test, since this species is very closely related to *A. koa*, with very low genetic divergence between the two species (Brown et al. 2012). Field trials using caged caterpillars on live plants could also be employed, to determine whether

caterpillar responses to cut foliage in the lab are representative of responses to live plants.

The substantial variation in survival and development time we observed among different diets and temperatures suggests that many factors affect performance of the koa looper, and it is likely that these all may affect population fluctuations. Further research examining the factors influencing koa looper performance, along with monitoring of populations, would provide a better understanding of factors contributing to the natural outbreaks of this important native insect.

Acknowledgments

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